Changes in the freshwater mussel communities of Lake Pepin, Upper Mississippi River, Minnesota and Wisconsin, 1990-1997

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Abstract: Densities of unionid mussels were measured at 7 mussel beds in Lake Pepin, Upper Mississippi River Mile (MRM) 784.2 - 764.5, Minnesota and Wisconsin, from 1990 to 1997. Densities of the commercially harvested threeridge, *Amblema plicata*, declined at 5 of the 7 mussel beds sampled. The most dramatic decline occurred at the Hok Si La, Minnesota, mussel bed where densities of *A. plicata* averaged about 22 mussels/m^2 in 1993, and declined to ≤6/m^2 between 1995-97 ($F=14.940$, $df=4$, $P<0.0001$). Densities of non-harvested mussel species remained constant at all but one bed during this research project. Shell height distributions for *A. plicata* indicate that there is little or no recent recruitment evident for this species within the sampled mussel beds of Lake Pepin. During this study, zebra mussels *(Dreissena polymorpha)* became established in Lake Pepin. The greatest density of *D. polymorpha* was found in the downstream portion of the lake, where they had been steadily increasing, reaching average densities of over 4,000 mussels/m^2 in 1997. Our results suggest that commercial harvest of *A. plicata* is having a negative impact upon their populations within Lake Pepin. We suggest that the findings of the present study, along with population estimates of *A. plicata* and *D. polymorpha*, be incorporated into management recommendations that will ensure the continued survival of *A. plicata* populations into the future.

Key Words: Unionidae, Dreissenidae, harvest

Lake Pepin, a 40 km long natural widening of the upper Mississippi River between Minnesota and Wisconsin, historically harbored a diverse freshwater mussel assemblage (Wilson and Danglade, 1914; Grier, 1922; Grier and Mueller, 1922; Southall, 1925; Ellis, 1931). A decline in unionid population densities in Lake Pepin began in the early 1900s and has been attributed to commercial harvest, water pollution originating from the Twin Cities, Minnesota, and habitat degradation (Grier, 1922; Southall, 1925; Ellis, 1931; Fuller, 1978; Thiel, 1981).

Because some mussel species residing in Lake Pepin are commercially valuable, and therefore harvested for the cultured pearl industry, there is concern that over-harvesting may again be occurring. Fuller (1978), Williams *et al.* (1993), and Anthony and Downing (2001) speculated that declines in certain populations of mussels can be directly related to over-harvesting, with these mussels now present in low numbers due to their inability to recover from historical harvesting pressures.

While harvesting removes individuals of select species, a more recent threat to all unionid species is caused by the introduction of the zebra mussel, *Dreissena polymorpha* (Pallas, 1771). With the recent introduction of *D. polymorpha* into Lake Pepin, there is a concern that it may cause declines in native mussel populations in the Upper Mississippi River as it has in other regions of North America (Ricciardi *et al.*, 1995; 1998; Hart, 1999; Hart *et al.*, 2001a, 2001b).

Because of concern that over-harvest of at least one unionid species, *Amblema plicata* (Say, 1817), may be occurring within Lake Pepin, a long-term monitoring study of mussel beds was initiated in 1990. Monitoring was undertaken to provide a quantitative assessment of unionid populations with each of seven mussel beds. An added dimension of this monitoring program became necessary with the introduction of *Dreissena polymorpha* into Lake Pepin. Therefore, this research was modified to include the measurement of population densities of *D. polymorpha* that are currently colonizing Lake Pepin.

METHODS

Study sites

Seven unionid mussel beds were sampled annually from 1990 to 1997 in Lake Pepin, Minnesota (Fig. 1). Sampled beds located within Lake Pepin were located near

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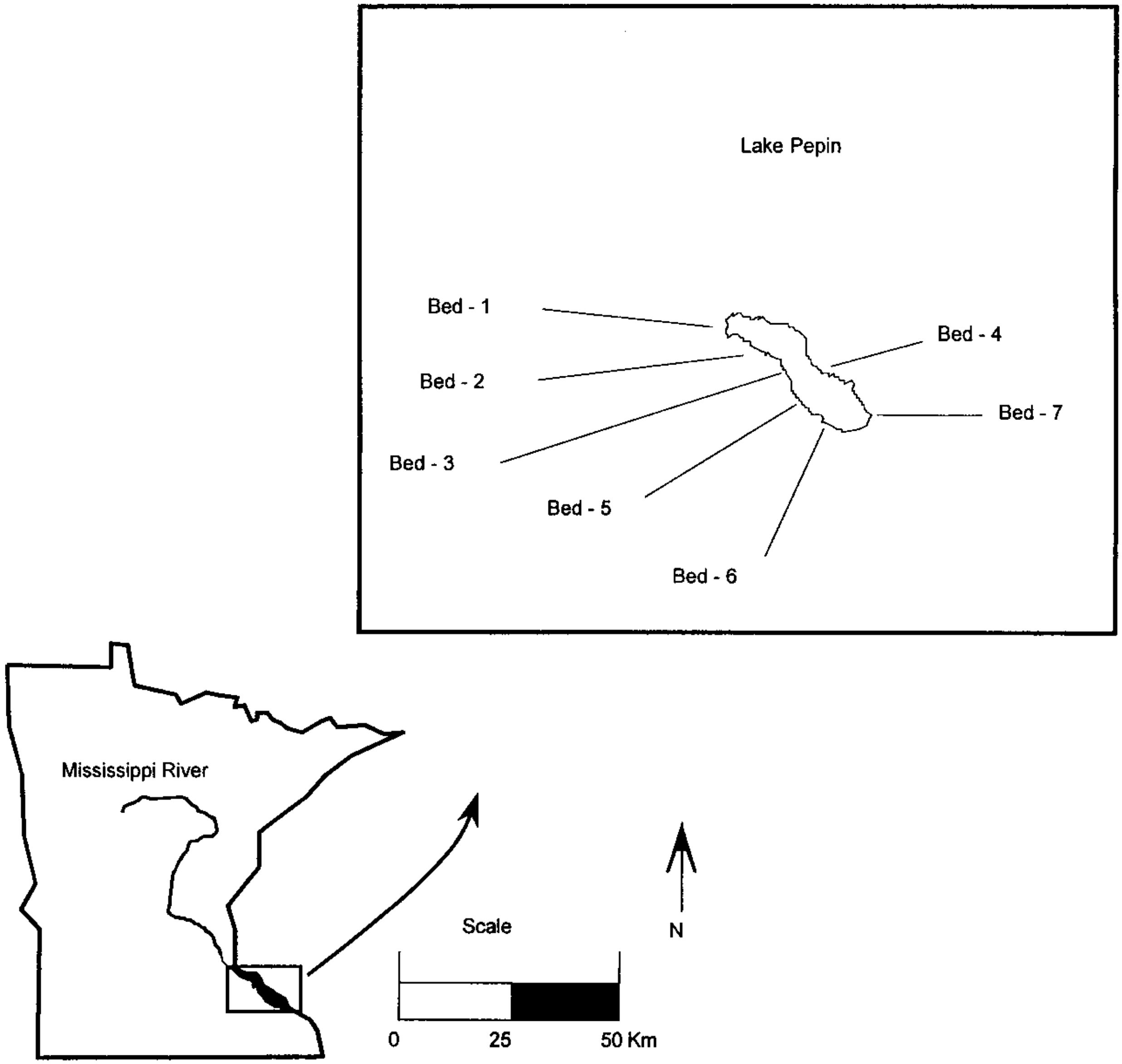

Fig. 1. Location of Lake Pepin between Minnesota and Wisconsin. Map inset shows locations of mussel beds where quantitative and qualitative samples were collected.

Fredrich's Point at Mississippi River Mile (MRM) 784.2 (Bed-1), Methodist Point at MRM 779.2 (Bed-2), Hok Si La at MRM 776 (Bed-3), Erickson's Point at MRM 775.5 (Bed-4), Waterman's at MRM 774 (Bed-5), King's Coulee at MRM 767.2 (Bed-6), and at the outlet of Lake Pepin along the Wisconsin shore across the river from Lacupolis, Minnesota, MRM 764.5 (Bed-7).

Mussel sampling

The quantitative methods that were used for the collection of unionid mussels during this study are outlined by Isom and Gooch (1986), Kovalak *et al.* (1986), Miller and Payne (1995), and references therein. Quantitative quadrat samples were collected at 7 beds by divers using SCUBA. At each bed, 3 subsites were randomly chosen for sampling. At each subsite, 10 randomly placed 0.25 m^2 aluminum quadrats were searched for mussels. Mussels were collected from within each of the quadrats either by placing all of the substrate, excavated to a depth of about 15 cm, into 20 L plastic pails and sieving the sample through a 0.6 cm^2 screen, or with the use of a suction dredge. When using the dredge, substrate from each quadrat was pumped to the surface, sieved through a 0.6 cm^2 screen, and searched for live mussels (Miller and Payne, 1995). All live mussels were removed from the screens and placed in labeled bags. Divers also collected qualitative samples during timed searches, placing all the mussels they encountered into mesh bags.

All collected mussels were identified, aged by counting the annual growth rings on the exterior of the shells' surfaces, measured for total shell length and height, and returned back into the substrate unharmed (Cvancara, 1970). Mussel identifications are based on taxonomic descriptions provided by Cummings and Mayer (1992). Taxonomy is that of Turgeon *et al.* (1998).

Data were analyzed using the statistical software program SYSTAT (Wilkinson *et al.*, 1992). A one-way analysis of variance and a post-hoc Tukey's multiple comparison technique were used to detect changes in mussel density over the course of this study.

While the weight of *Amblema plicata* harvested is of interest, a more useful management statistic is the number of individual *A. plicata* that are actually being removed from the Lake Pepin population. We developed regression equations for shell height vs. shell mass for *A. plicata* collected from both Minnesota and Wisconsin mussel beds. Using these regression equations we were able to calculate the number of legal-sized *A. plicata* per pound. This allowed us to estimate the number of individual *A. plicata* that have been harvested from Lake Pepin. Relationships between age, shell length, shell height, and shell mass of *A. plicata* were analyzed with the use of regression analysis (Zar, 1984). Linear, power, logarithmic, and exponential regression equations were investigated, and equations expressing the best fit to the data are presented (Smock, 1980).

RESULTS

The main goal of this research was to quantify changes within mussel beds. Therefore, we did not conduct statistical analyses on the differences among beds. The analysis of mussel community changes are presented with the upstream-most mussel beds and progressing sequentially to the downstream-most bed. While numerous mussel species may have been collected from a particular bed, we conducted statistical analysis only on those species that were present in sufficient enough numbers to warrant analysis (> 30 individuals collected).

Community composition

Twenty-nine unionid species were collected from the 7 mussel beds over the 8 years of this study. Bed-7, the downstream-most bed sampled, had the highest species richness, 29 species, compared to only 12 species at Bed-2, one of the most upstream beds sampled (Table 1, Fig. 1). Fourteen mussel species were collected from quantitative samples at Bed-1, while 12 mussel species were collected from Bed-2 during the study (Table 1). Both quantitative and qualitative sampling yielded 16 species in the Bed-3 community, while 15 mussel species comprised the Bed-4 community (Table 1). A total of 17 mussel species was collected from Bed-5 using both types of sampling, while the mussel community at Bed-6 comprised 13 species, and Bed-7 had 29 species (Table 1).

During the last year of quantitative sampling *Amblema plicata* remained the dominant mussel species in all beds sampled (Table 2). *Fusconaia flava* (Rafinesque, 1820) was the second most dominant mussel species in 5 of the 7 beds. *Elliptio dilatata* (Rafinesque, 1820), a species of special concern in the state of Minnesota, was the second most dominant mussel species in only one of the mussel beds (Bed-7) (Table 2). *Lampsilis siliquoidea* (Barnes, 1823), *Lampsilis cardium* (Rafinesque, 1820), and *Truncilla truncata* (Rafinesque, 1820), increased in dominance, while species such as *A. plicata*, and *Obliquaria reflexa* (Rafinesque, 1820), tended to decrease in dominance from upstream sites to downstream sites.

Mussel density

Densities of mussel communities ranged from a high of >70/m^2 at Bed-7 in 1993 to < 8/m^2 at Bed-5 in 1996 (Table 3). Densities of commercially harvested mussels, as well as protected species, did not show any appreciable changes in population density from 1995-97 within Bed-1 ($F = 2.677$, df=2, $p = 0.073$) (Table 3).

There was, however, a significant decline in mussel community density within Bed-2 over time ($F = 23.790$, df =3, $p<0.0001$) (Table 3). The mussel community density within Bed-3 was found to be declining over the course of this study ($F = 21.045$ df=4, $p<0.0001$) (Table 3). A decline in mussel community density was also measured in Bed-4 ($F = 3.315$, df=2, $p = 0.042$). Densities in Bed-4 in 1994 were 31.5/m^2, dropping to 21.3/m^2 in 1996 (Table 3). The community density of Bed-5 showed significant declines, decreasing from 19.6 mussels/m^2 in 1991, dropping to a low of 8.8/m^2 in 1996 ($F = 7.681$, df=3, $p<0.0001$) (Table 3). Mussel density within Bed-6 did not change significantly, remaining near 12 mussels/m^2 from 1995-97 ($F = 0.776$, df 2, $p = 0.463$) (Table 3). During this study Bed-7, the most downstream bed sampled, had the highest mussel densities measured within Lake Pepin. Density of this community was 70.6 mussels /m^2 in 1993, declining by 50%, to 34.7/m^2 in 1997 ($F=16.646$, df=3, $p<0.0001$) (Table 3).

Since reporting densities of all of the mussel species combined may be misleading, i.e., an increase in density of species A may mask a decrease in density of species B, we

Table 1. Live unionid species collected in quantitative and qualitative samples from Lake Pepin, Minnesota and Wisconsin, 1990 - 97.

	Mussel Beds[1]						
Mussel Species	1	2	3	4	5	6	7
Subfamily Ambleminae							
Megalonaias nervosa	x	x	x		x		x
Tritogonia verrucosa							x
Quadrula quadrula	x						
Quadrula metanevra					x		x
Quadrula pustulosa	x	x	x	x	x	x	x
Amblema plicata	x	x	x	x	x	x	x
Fusconaia flava	x	x	x	x	x	x	x
Cyclonaias tuberculata							x
Pleurobema coccineum					x		x
Elliptio diltata			x	x	x	x	x
Subfamily Anodontinae							
Utterbackia imbecillis	x	x	x	x	x		x
Pyganodon grandis		x	x			x	x
Stophitus undulatus			x		x		x
Alasmidonta marginata							x
Lasmigona complanata							x
Lasmigona costata							x
Subfamily Lampsilinae							
Obliquaria reflexa	x	x	x	x	x	x	x
Actinonaias ligamentina							x
Ellipsaria lineolata							x
Obovaria olivaria				x			x
Truncilla truncata	x	x	x	x	x	x	x
Truncilla donaciformis							x
Leptodea fragilis	x	x		x			x
Potamilus ohiensis	x	x	x	x	x	x	x
Potamilus alatus	x		x	x	x	x	x
Toxolasma parvus	x		x	x	x	x	x
Ligumia recta			x	x	x	x	x
Lampsilis siliquoidea	x	x	x	x	x	x	x
Lampsilis cardium	x	x	x	x	x	x	x
Total number of species collected	14	12	16	15	17	13	29

[1]Bed 1 = Fredrich's Point, bed 2 = Methodist Point, bed 3 = Hok Si La, bed 4 = Erickson's Point, bed 5 = Waterman's, bed 6 = King's Coulee, and bed 7 = Lacupolis.

separately analyzed species within the community to determine if species-specific density increases or declines were apparent. Likewise, because *Amblema plicata* is commercially harvested from Lake Pepin, we analyzed this species three ways; all *A. plicata* combined; individuals of legal harvest size (≥70 mm in shell height); and individuals of sub-legal size (< 70 mm in shell height).

Densities of all *Amblema plicata* remained stationary at only 2 of the beds, and declined at 5 of the 7 mussel beds sampled. Densities of *A. plicata* remained unchanged from 1995-97 within Bed-1 ($F=0.809$, $df=2$, $P=0.448$) (Table 3). Legal-sized *A. plicata* and individuals of sub-legal size remained unchanged as well ($F = 0.617$, $df=2$, $p = 0.541$, and $F = 0.792$, $df=2$, $p = 0.456$, respectively) (Table 1). Similarly, the density of *A. plicata* within Bed-6 did not change significantly during this study, remaining near $8/m^2$ from 1995-1997 ($F = 2.287$, $df=2$, $p = 0.108$). Accordingly, both legal and sub-legal *A. plicata* densities did not change in any significant manner ($F= 0.384$, $df=2$, $p=0.682$, and $F=1.807$, $df=2$, $p=0.170$, respectively) (Table 3).

The overall change in mussel density in Bed-2 noted previously was most likely the result of declining population sizes of *Amblema plicata*. This population of *A. plicata* declined significantly from 1993-97 ($F = 21.350$, $df=3$, $p<0.0001$). Densities of this species within Bed-2 were $15.3/m^2$ in 1993 compared to $5.1/m^2$ in 1997 (Table 3). Legal-sized *A. plicata* did not decline ($F = 0.851$, $df=3$, $p = 0.468$), whereas sub-legal sized individuals did ($F = 20.158$, $df=3$, $p<0.0001$) (Table 3). Similar to Bed-2, densities of *A. plicata* within Bed-3 ranged from $21.8/m^2$ in 1993 to $3.3/m^2$ in 1997 ($F = 14.940$, $df=4$, $p<0.0001$). Densities of legal-sized individuals of *A. plicata* within Bed-3

Table 2. Percent occurrence of mussel species collected from quantitative samples during the last sampling event (1996 or 1997). Values are rounded to the nearest whole percentage point.

Species	Bed 1 % occurrence	Bed 2 % occurrence	Bed 3 % occurrence	Bed 4 % occurrence	Bed 5 % occurrence	Bed 6 % occurrence	Bed 7 % occurrence
Amblema plicata	64	46	50	57	59	37	31
Fusconaia flava	6	32	24	12	19	34	5
Obliquaria reflexa	19	14	8	11	12	7	9
Utterbackia imbecillis	1	3	0	2	0	0	1
Truncilla truncata	8	2	10	12	4	12	14
Lampsilis siliquoidea	1	2	2	0	2	1	3
Toxolasma parvus	1	1	0	0	0	5	1
Quadrula pustulosa	1	1	2	2	1	1	1
Potamilus ohiensis	1	1	1	1	0	0	1
Pyganodon grandis	0	1	1	0	0	1	1
Strophitus undulatus	0	0	0	0	0	0	2
Quadrula quadrula	0	0	0	0	0	1	0
Potamilus alatus	0	0	0	0	0	0	1
Pleurobema coccineum	0	0	0	0	0	0	1
Megalonais nervosa	0	0	2	0	0	0	0
Leptodea fragilis	0	0	0	0	0	0	2
Lampsilis cardium	0	0	1	2	1	0	7
Ligumia recta	0	0	0	0	1	0	2
Elliptio dilatata	0	0	1	0	0	0	20

declined from 9.6/m^2 in 1990 to 0.8/m^2 in 1997 (F = 12.574, df=4, $p<0.0001$). Individuals < 70mm declined from 1993 to 1995-97 (F = 13.843, df=4, $p<0.0001$); however, multiple comparison tests revealed no differences in densities comparing 1990 to 1995-97 ($P>0.05$) (Table 3).

Mussel community density declines within Bed-4 were most likely due to changes in *Amblema plicata* densities. Densities of *A. plicata* declined from 18.3/m^2 and 19.3/m^2 in 1991 and 1994 to 12.3/m^2 in 1996 (F = 4.472, df=2, p = 0.015) (Table 3). While densities of legal-sized *A. plicata* did not change during this study (F = 1.432, df=2, p = 0.242) (Table 3), densities of sub-legal sized *A. plicata* declined from 17.6/m^2 in 1991 to 10.3/m^2 in 1996 (F = 6.567, df=2, p = 0.002).

The change in mussel community densities at Bed-5 can also be attributed to population declines of the harvested mussel species, *Amblema plicata*, which dropped from 11.8/m^2 in 1991 to 6.4/m^2 in 1997 (F = 6.228, df=3, p = 0.001). Legal-sized *A. plicata* did not show signs of population declines (F = 1.282, df=3, p = 0.285), yet individuals of sub-legal size in the population did (F = 5.575, df=3, p = 0.001) (Table 3).

Densities of all *Amblema plicata* in Bed-7 were 18.5/m^2 in 1993 and dropped to 7.7/m^2 in 1996 (F = 4.512, df=3, p = 0.005) (Table 3). Densities of both legal and sub-legal *A. plicata* in this bed also fluctuated during this study, albeit not significantly between some years (F = 2.873, df=3, p = 0.040, and F = 4.379, df=3, p = 0.006, respectively) (Table 3).

The population density of the commercial mussel species *Fusconaia flava* showed slight fluctuations or remained stationary at 5 of the 7 beds sampled, and declined at the other 2 beds sampled. Densities of *F. flava* in Bed-1 declined in 1997 compared to 1996, yet there was no significant difference in densities between 1995 and 1997 (F = 7.065, df=2, p = 0.001) (Table 3). Densities peaked with 3.07 mussels/m^2 in 1996 compared to a low of 0.7/m^2 in 1997. Similarly, *F. flava* in Bed-3 showed a significant decline in numbers during select years from 1990 to 1997 (F = 6.735, df=4, $p<0.0001$) (Table 3).

Fusconaia flava, a species legally harvested from Wisconsin waters of the Mississippi River, showed significant declines from 1993-97 within Bed-7 (F = 22.897, df=3, $p<0.0001$). Densities of this species declined from 9.7/m^2 in 1993 to 1.6/m^2 in 1996-97 (Table 3).

Fusconaia flava did not show any significant differences in density during this study in Bed-2 (F = 2.638, df=3, p = 0.052) (Table 3). Likewise, there were no significant differences in densities of *F. flava* detected from 1991 to 1996 in Bed-4. Densities within Bed-4 were 2.9/m^2 in 1991 and remained close to this level through 1996 (F = 0.292, df=2, p = 0.748) (Table 3). Unlike the commercially valuable *Amblema plicata*, it is illegal to harvest *F. flava* from Minnesota waters. Consequently *F. flava* did not show any significant declines in density from 1991-97 within Bed-5 (F = 0.870, df 3, p = 0.460) remaining near 2-3 individuals/m^2 (Table 3). Likewise, densities of *F. flava* did not show any significant changes during the time Bed-6 was studied, remaining near 2.5 - 4 mussels/m^2 from 1995-97 (F = 2.412, df=2, p = 0.096) (Table 3).

Although *Fusconaia flava* exhibited some density declines in Bed-1, *Obliquaria reflexa* did not. *Obliquaria*

Table 3. Mean density (± SE) comparisons of Lake Pepin unionid populations within mussel beds. Multiple comparisons are made using ANOVAs and Tukey's multiple comparison tests. Means are based on 30 replicate 0.25 m^2 quadrat samples.

	1990		1991		1993		1994		1995		1996		1997	
Site and Species	Mean (SE) [2]	Mult. [1] comp.	Mean (SE) [2]	Mult. [1] comp.	Mean (SE) [2]	Mult. [1] comp.	Mean (SE) [2]	Mult. [1] comp.	Mean (SE) [2]	Mult. [1] comp.	Mean (SE) [2]	Mult. [1] comp.	Mean (SE) [2]	Mult. [1] comp.
Bed-1														
All unionids									13.2 (1.69)	A	15.9 (1.17)	A	11.7 (1.02)	A
A. plicata									7.07 (0.83)	A	8.8 (1.11)	A	7.5 (0.76)	A
A. plicata > 70 mm[3]									0.7 (0.34)	A	0.5 (0.25)	A	0.4 (0.16)	A
A. plicata < 70 mm[3]									6.5 (0.83)	A	8.27 (1.03)	A	7.1 (0.76)	A
F. flava									2.3 (0.68)	AB	3.07 (0.71)	A	0.7 (0.25)	B
O. reflexa									2.7 (0.48)	A	2.13 (0.71)	A	2.2 (0.43)	A
Bed-2														
All unionids					27.1 (2.4)	A			25.7 (1.87)	AB	19.6 (1.69)	B	11.3 (0.98)	C
A. plicata					15.3 1.99)	A			15.7 (1.34)	A	9.5 (1.01)	B	5.1 (0.66)	C
A. plicata > 70 mm[3]					0.53 (0.25)	A			0.8 (0.35)	A	0.27 (0.19)	A	0.4 (0.16)	A
A. plicata < 70 mm[3]					14.8 (2.0)	A			14.8 (1.27)	A	9.6 (1.04)	B	4.8 (0.66)	C
F. flava					6.3 (0.93)	A			5.6 (0.44)	A	4.4 (0.78)	A	3.7 (0.59)	A
O. reflexa					4.3 (0.90)	A			3.47 (0.81)	AB	4.8 (0.82)	A	1.5 (0.34)	B
Bed-3														
All unionids	30.4 (5.69)	A			29.2 (4.3)	A			11.2 (1.53)	B	11.6 (1.24)	B	6.8 (0.65)	B
A. plicata	16.8 (3.76)	AB			21.8 (4.67)	A			6.0 (1.28)	BC	5.0 (0.76)	C	3.3 (0.56)	C
A. plicata > 70 mm[3]	9.6 (3.59)	A			4.1 (1.17)	B			0.8 (0.35)	C	0.6 (0.34)	C	0.8 (0.23)	C
A. plicata < 70 mm[3]	7.2 (0.99)	A			17.6 (3.53)	B			5.2 (1.09)	AC	4.4 (0.78)	AC	2.5 (0.49)	AC
F. flava	7.6 (1.83)	A			3.5 (0.83)	BC			4.1 (0.68)	AC	4.3 (0.85)	AC	1.7 (0.33)	B
O. reflexa	0.8 (0.53)	AB			0.27 (0.19)	A			0.27 (0.19)	A	1.4 (0.47)	B	0.53 (0.20)	AB
Bed-4														
All unionids			23.7 (2.05)	AB			31.5 (3.03)	A			21.3 (2.69)	B		
A. plicata			18.3 (1.7)	A			19.3 (1.76)	A			12.3 (1.79	B		

(continued)

Table 3. (continued)

Site and Species	1990 Mean (SE)[2]	1990 Mult.[1] comp.	1991 Mean (SE)[2]	1991 Mult.[1] comp.	1993 Mean (SE)[2]	1993 Mult.[1] comp.	1994 Mean (SE)[2]	1994 Mult.[1] comp.	1995 Mean (SE)[2]	1995 Mult.[1] comp.	1996 Mean (SE)[2]	1996 Mult.[1] comp.	1997 Mean (SE)[2]	1997 Mult.[1] comp.
A. plicata > 70 mm[3]			1.6 (0.45)	A			0.5 (0.34)	A			1.5 (0.41)	A		
A. plicata < 70 mm[3]			17.6 (1.72)	A			18.8 (1.92)	A			10.3 (1.8)	B		
F. flava			2.9 (0.81)	A			3.8 (1.00)	A			2.8 (0.72)	A		
O. reflexa			1.7 (0.42)	A			4.3 (0.85)	B			2.4 (0.65)	AB		
Bed-5														
All unionids			19.6 (3.00)	A			16.6 (1.77)	AB			8.8 (1.16)	C	10.8 (1.34)	BC
A. plicata			11.8 (2.40)	A			11.8 (1.65)	AB			4.8 (0.87)	C	6.4 (0.97)	BC
A. plicata > 70 mm[3]			1.8 (0.74)	A			2.3 (0.81)	A			0.9 (0.31)	A	1.2 (0.34)	A
A. plicata < 70 mm[3]			10 (2.08)	A			9.4 (1.66)	AC			3.9 (0.89)	B	5.1 (0.81)	BC
F. flava			2.8 (0.66	A			2.3 (1.09)	A			1.5 (0.41)	A	2.0 (0.53)	A
Bed-6														
All unionids									15.7 (1.36)	A	15.2 (1.81)	A	13.2 (1.33)	A
A. plicata									7.9 (1.08)	A	6.9 (1.08)	A	4.9 (0.78)	A
A. plicata > 70 mm[3]									0.93 (0.31)	A	0.8 (0.35)	A	0.5 (0.32)	A
A. plicata < 70 mm[3]									6.9 (1.08)	A	5.9 (0.95)	A	4.4 (0.78)	A
F. flava									2.5 (0.56)	A	4.7 (0.90)	A	4.5 (0.81)	A
O. reflexa									0.93 (0.31)	A	0.4 (0.22)	A	0.93 (0.37)	A
Bed-7														
All unionids					70.56 (4.79)	A			36.1 (4.36)	B	30.1 (2.86)	B	34.7 (4.10)	B
A. plicata					18.5 (2.74)	A			16.8 (2.74)	A	7.7 (1.47)	B	10.9 (2.23)	AB
A. plicata > 70 mm[3]					2.3 (0.77)	A			1.2 (0.48)	A	2.0 (0.76)	A	0.13 (0.13	A
A. plicata < 70 mm[3]					13.9 (2.64)	AB			15.6 (2.60)	AC	5.4 (1.09)	B	11.1 (2.23)	AB
F. flava					9.7 (1.48)	A			2.7 (0.62)	B	1.6 (0.41)	B	1.6 (0.53)	B
E. dilatata					9.9 (1.35)	A			7.1 (1.08)	A	8.9 (1.38)	A	6.8 (1.09)	A

[1] Means with a common letter within both sites and species are not significantly different, (P>0.05), using an ANOVA and Tukey's multiple comparison tests.
[2] (SE) equals standard error of the mean.
[3] Shell height in mm.

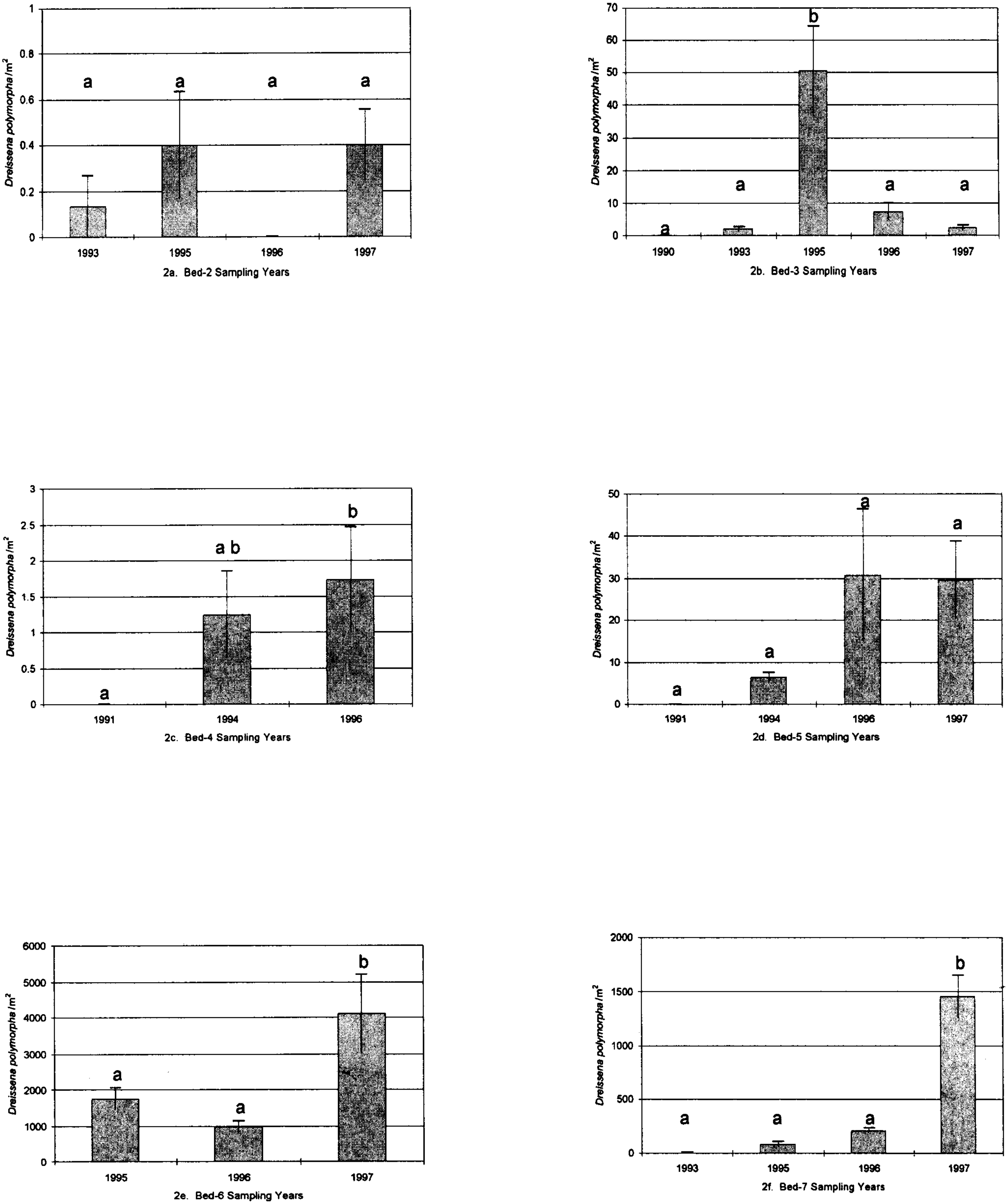

Fig. 2. Densities of *Dreissena polymorpha* measured in Beds 2-7. Similar letters above histograms indicate a lack of significant differences among years (mean ± 1 SE; ANOVA and Tukey's multiple comparison test, P>0.05).

reflexa densities were stable in Bed-1 from 1995-96, remaining near 2.5 mussels/m^2 ($F = 0.247$, df=2, $p = 0.782$) (Table 3). *Obliquaria reflexa* showed a somewhat different pattern in Bed-2 in that population densities gradually declined from 1993 to 1997 ($F = 5.808$, df=3, $p = 0.001$) (Table 3). The between-year fluctuations in density of *O. reflexa* in Bed-3 were similar to those of *F. flava* in that there were some significant differences between years; densities in 1990 and 1997 were 0.8/m^2 and 0.53/m^2, respectively ($F = 2.570$, df=4, $p = 0.04$) (Table 3). *Obliquaria reflexa* in Bed-4 showed slight changes in density during this study ($F = 3.507$, df=2, $p = 0.035$). Densities in Bed-4 were 1.7/m^2 in 1991, increasing to 4.3/m^2 in 1994, and declining again to 2.4/m^2 in 1996 (Table 3).

Densities of *Obliquaria reflexa* in Bed-6 were much the same throughout this study. Its densities have been rather stable, albeit low, < 1 mussel/m^2, with no significant differences being detected from 1995-97 ($F = 1.002$, df=2, $p = 0.371$) (Table 3).

Elliptio dilatata, a species found in large numbers only in Bed-7, did not change significantly in population density from 1993-1997 ($F = 1.327$, df=2, $p = 0.270$). Densities of this species within Bed-7 stayed near 7-9 mussels/m^2 throughout the present study (Table 3).

Dreissena polymorpha was initially collected from Bed-1 in 1995 and has been found in low numbers since that time, <0.03/m^2. *Dreissena polymorpha* was initially collected from Bed-2 in 1993, and was present in low numbers through 1997, although densities did not change significantly ($F = 1.431$, df=3, $p = 0.236$) (Fig. 2a). However, there were significant differences in densities of *D. polymorpha* at Bed-3, declining from a peak of 50/m^2 in 1995 to <10/m^2 in 1997 ($F = 12.119$, df=4, $p<0.0001$) (Fig. 2b). *Dreissena polymorpha* was first collected in 1994 in Bed-4, yet densities did not significantly increase during this study ($F = 3.076$, df=2, $p = 0.052$) (Fig. 2c). Likewise, *D. polymorpha* was first found in low numbers in Bed-5 in 1991, and population densities did not change significantly from 1991-97 ($F = 1.769$, df=3, $p = 0.159$) (Fig. 2d).

The greatest change in the mussel community noted within Bed-6 was the increase in density of *Dreissena polymorpha*. Densities within Bed-6 were >1,700 mussels/m^2 in 1995, increasing to over 4,100 mussels/m^2 in 1997 ($F = 6.314$, df=2, $p = 0.003$) (Fig. 2e). *Dreissena polymorpha* is still increasing in this bed, as we have noted large numbers of newly settled individuals during the summers of 1999 and 2000 (Hart and Davis, personal observation). In the species rich Bed-7 community, *D. polymorpha* was first collected in 1993, and densities have been increasing since their initial occurrence ($F = 39.173$, df=3, $p<0.0001$). *Dreissena polymorpha* increased from less than 4/m^2 in 1993 to over 1,400/m^2 in 1997 (Fig. 2f).

***Amblema plicata* recruitment**

Because one of the objectives of this study was to assess the health of the *Amblema plicata* populations in Lake Pepin, we noted the occurrence of young *A. plicata* within the study areas. Shell height distributions of *A. plicata* indicated recent recruitment into the studied populations is occurring only at low levels.

We measured small numbers of young individuals within several of the sampled beds, but most populations were dominated by older individuals, indicating that significant recent recruitment has not occurred. Histograms of shell height from Bed-3 and Bed-7 (Figures 3 and 4 respectively) illustrate typical shell height distributions of *Amblema plicata* measured within all of the mussel beds sampled during this study.

Using Minnesota data (Hart, 1999), the number of legal-sized *Amblema plicata* per pound equaled 2.03 individuals (Fig. 5), while the number of individuals per pound using Wisconsin regression equations (Hart, 1999; Fig. 6) equaled 2.08. Using the harvest records acquired from the Minnesota and Wisconsin Departments of Natural Resources (Fig. 7) (Welke and Miller, 1990; Hart, 1999; Minnesota and Wisconsin DNR unpublished data) and the regression equations we developed, we estimate that about 254,000 live mussels were harvested from the Minnesota side of Lake Pepin in 1993, and an additional 750,000 mussels were taken from the Wisconsin side in 1990.

DISCUSSION

Lake Pepin still harbors a diverse mussel assemblage. Twenty-nine living unionid species were collected from this portion of the Mississippi River. The downstream-most mussel bed sampled, Bed-7, possessed a community with populations of all of the species that were collected from Lake Pepin during the present study. We also observed that the numbers of mussel species living within Lake Pepin tended to increase from upstream to downstream. The upstream and mid-lake habitats of Lake Pepin have been impacted more by water quality and habitat degradation (Ellis, 1931; Thiel, 1981), when compared to those downstream. This is particularly true of Bed-7, which is at the outlet of Lake Pepin and is more a "riverine" habitat, benefitting from the sediment settling effects of the lake. This difference in habitats may explain in part why the downstream portion of the lake supports a more diverse mussel community at this time. The downstream-most mussel bed sampled not only had the most species present, but also had the highest density of all beds sampled. However, this bed, as well as four additional beds sampled, showed population density declines for some of the mussel species that inhabit these areas.

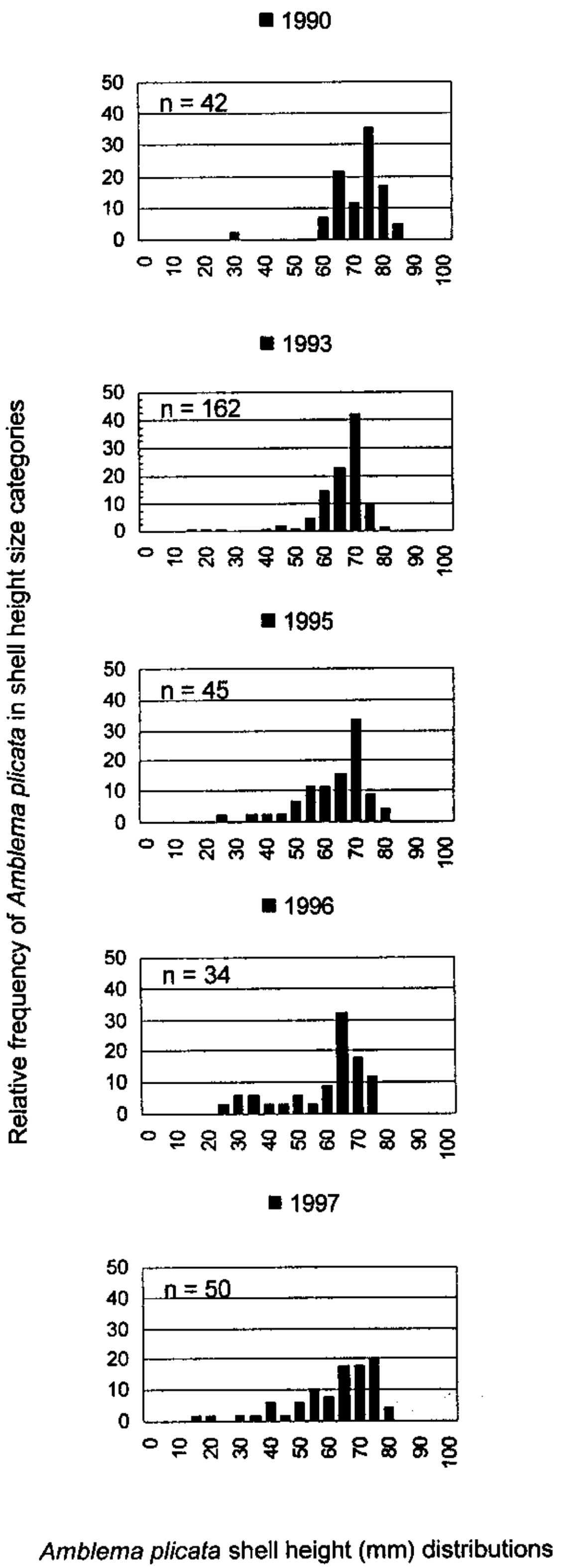

Fig. 3. Shell height distributions of *Amblema plicata* measured in Bed-3 in 1990, 1993, and 1995-1997. The values on the x axis are the midpoints for the distribution ranges.

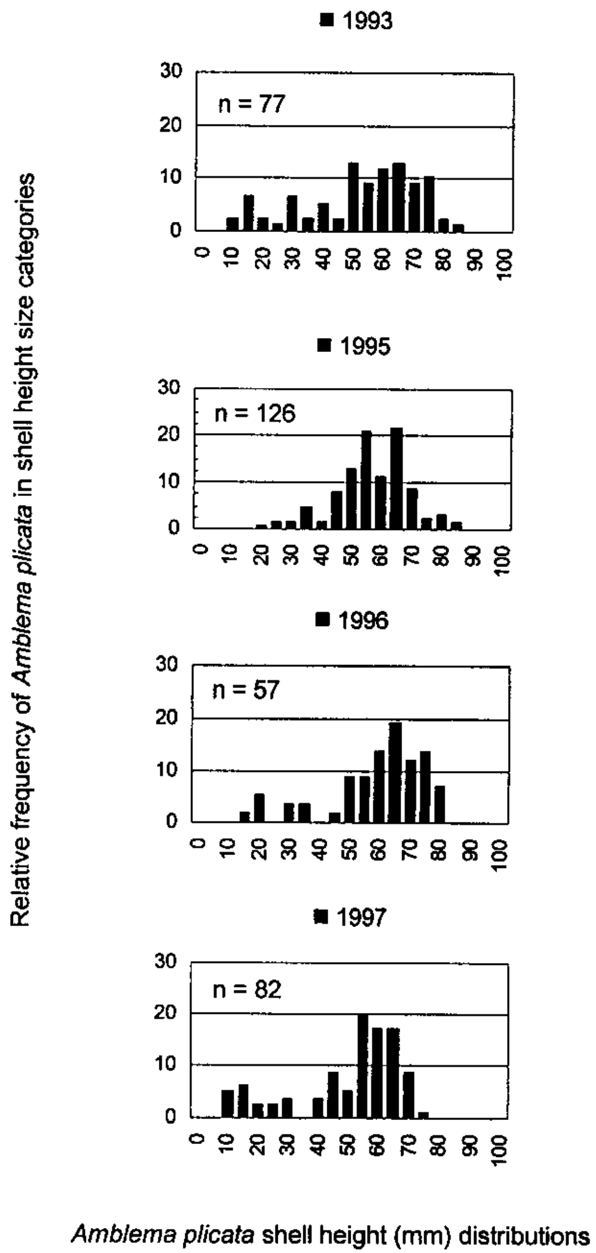

Fig. 4. Shell height distributions of *Amblema plicata* measured in Bed-7 in 1993 and 1995-1997. The values on the x axis are the midpoints for the distribution ranges.

Southall (1925) reported that during the early part of the 1900's, 35% of the Lake Pepin mussel community was comprised of the Lake Pepin mucket (*Lampsilis pepinensis*, now *Lampsilis siliquoidea* [Barnes, 1823]). Today *L. siliquoidea* is only represented as a minor component of the Lake Pepin mussel assemblage, making up less than 3% of the communities we sampled. The change in community dominance and density of *L. siliquoidea* within the Lake Pepin mussel assemblage was attributed to their commercial harvest for pearl buttons (Southall, 1925). Past harvesting pressure seems to be the most likely cause for the low numbers of this species as the present habitat conditions in Lake Pepin are favorable for *L. siliquoidea* (Hart, 1995). Currently the dominant mussel in the Lake Pepin community is the commercially harvested *Amblema plicata*. Yet its community dominance appears to be changing much as *L. siliquoidea* did.

Amblema plicata showed significant declines at 5 of the 7 mussel beds sampled during this study. At several of these sites density declines as great as 50% were detected. The most notable decline occurred at Bed-3 where densities of legal-sized *A. plicata* declined from a high of 9/m^2 to about 0.8 mussels/m^2 over the course of the present study. The most plausible explanation for the declines in legal sized individuals that we measured is their removal by commercial harvesters. We believe that the decline can be attributed to harvest because the mean annual survival of *A. plicata*, as well as other unionids in the habitats studied in Lake Pepin, has been shown to be relatively high in natural habitats (≥90%) (Hart, 1999; Hart *et al.*, 2001b), and large numbers of fresh dead *A. plicata* were not collected from any of these 5 mussel beds during routine sampling (Hart and Davis, personal observation). The lack of fresh dead individuals found at these sites indicate that the decline in population densities is not due to *Dreissena polymorpha*. We further believe that the declines in sub-legal sized *A. plicata* indicate that these individuals are either being harvested illegally or are being removed from the population when they grow into the legal harvest-size slot and are not being replaced by recruitment of new individuals into the population. The decline in densities we measured is the result of these individuals being physically removed from the populations. This type of population response, i.e., declining average sizes near to or at the age of first reproduction (Anthony and Downing, 2001), which is about 8 years of age for *A. plicata*, is typical for exploited populations. Large numbers of commercial harvesters were seen working at Beds 3 and 7 during the late 1980s (Davis, personal observation), and harvesters were often present during the summer months of this research project (Hart, personal observation).

The other noteworthy change in the population structure of *Amblema plicata* came from Bed-7, where densities of this species were over 18 mussels/m^2 in the early 1990s and declined to less than 9/m^2 during the late 1990s. During this study this mussel bed was harvested for not only *A. plicata*, but also *Fusconaia flava* (Hart, personal observation). Densities of *F. flava* also declined at this bed, where densities were over 9/m^2 during 1991, declining to 2/m^2 in 1997.

While *Fusconaia flava* are legal to harvest from Wisconsin border waters, it is not legal to harvest this

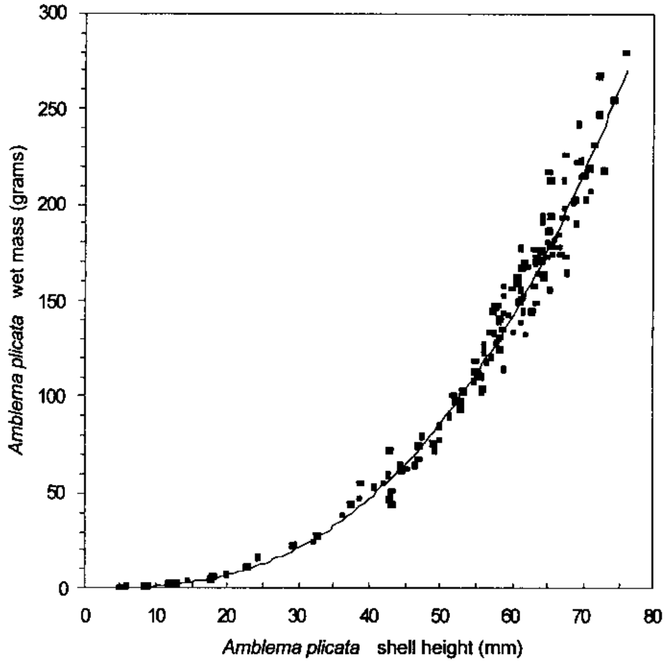

Fig. 6. Shell height vs. mass relationships of *Amblema plicata* measured in Bed-4 (Wisconsin) (Hart, 1999). Power equation regression line fit to the data points equals: *Amblema plicata* shell mass = 0.0021(shell height)$^{2.7218}$. $R^2 = 0.9892$.

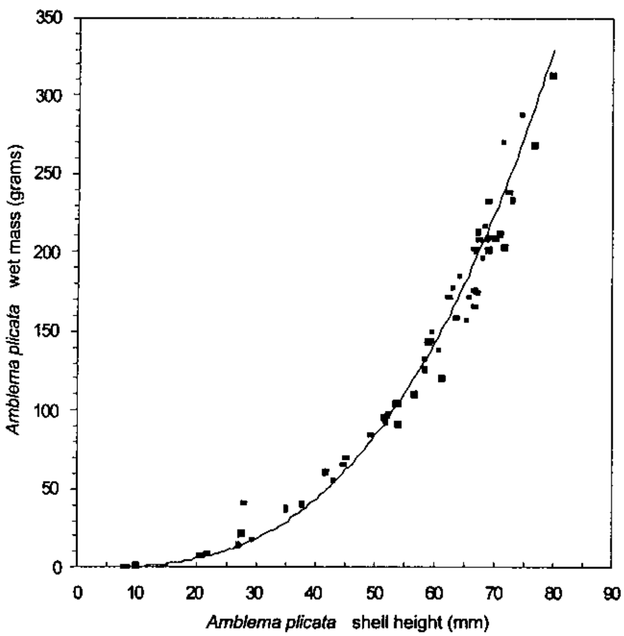

Fig. 5. Shell height vs. mass relationships of *Amblema plicata* measured in Bed-5 (Minnesota) (Hart, 1999). Power equation regression line fit to the data points equals: *Amblema plicata* shell mass = 0.0009(shell height)$^{2.9336}$. $R^2 = 0.9864$.

species in Minnesota. Densities of *F. flava* did not vary much at 4 of the 5 Minnesota beds studied. Other non-harvested mussel species, in both Minnesota and Wisconsin, showed either stationary or fluctuating densities during the time this study was conducted.

An assessment of the mussel harvest in the Mississippi River (Welke and Miller, 1990) revealed that over 360,000 pounds of live *Amblema plicata* were harvested from the Wisconsin portion of Lake Pepin in 1990. Welke and Miller (1990) speculated that this intense harvesting pressure could depress mussel stocks for several years. Minnesota Department of Natural Resources records since 1990 document the harvest of *A. plicata* from the Minnesota beds of Lake Pepin. These records reveal intense harvesting occurred in Minnesota waters as well. Harvest from Minnesota peaked in 1993, with approximately 125,000 pounds of mussels harvested (Minnesota Department of Natural Resources, unpublished data; Hart, 1999) (Fig. 7).

While the poundage of *A. plicata* harvested is of interest, a more useful management statistic is the number of individual *A. plicata* that are actually being removed from the Lake Pepin population. Applying the results of the regression equations we developed, we estimated that each pound of collected mussels equaled about two individuals. Therefore, using the harvest records from Lake Pepin and the results of the regression equations, we estimate that about 254,000 live mussels were harvested from the Minnesota side of Lake Pepin in 1993, and an additional 750,000 mussels were taken from the Wisconsin side in 1990. Given the large numbers of individuals removed from the lake in just these two years, as well as the findings of this study documenting declining population densities of *A. plicata* in Lake Pepin, Welke and Miller's (1990) concern that populations of this species may be reduced seems to be borne out. The constant population densities of non-harvested species and the decreasing populations of harvested species implicate commercial harvesting as a factor in these declines.

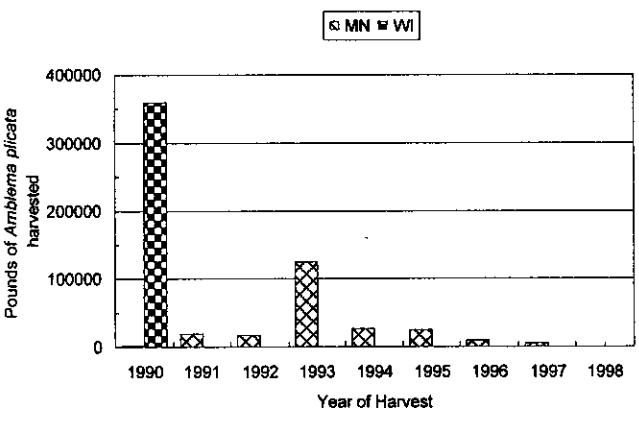

Fig. 7. Pounds of *Amblema plicata* harvested from Lake Pepin, Minnesota (Minnesota DNR unpublished data; Hart, 1999) and Wisconsin (Welke and Miller, 1990).

The ramifications of the harvesting of other molluscs have also been well documented. Declines in the commercially valuable mollusc, the black abalone (*Haliotis cracherodii*, Leach, 1814), in coastal California regions were attributed to their over-harvest (Richards and Davis, 1993). Much as we believe is occurring with *A. plicata* in Lake Pepin, *H. cracherodii* began to decline when increases in harvest occurred and recruitment could not keep pace with their removal (Richards and Davis, 1993). Heath *et al.* (1988) reported that there has been a steady decline in the commercially harvested washboard mussel, *Megalonaias nervosa* (Rafinesque, 1820), from some pools of the Upper Mississippi River. Commercial harvesting was implicated as a factor in the decline of *M. nervosa* because high levels of harvest had been documented, while low or no recruitment into the populations was evident (Heath *et al.*, 1988).

Size distributions of the *Amblema plicata* populations sampled during the present study indicate that there are very low levels of recruitment occurring for this species as well. Since *A. plicata* are like other long-lived organisms, sporadic recruitment may be able to maintain a population (Congdon *et al.*, 1994). However, sporadic recruitment was not readily detectable in appreciable numbers within most of the mussel beds we studied even though total substrate removal techniques were used to facilitate the collection of small individuals.

An additional factor that must be considered is not only the fate of *Amblema plicata* populations, but of all of the mussel species residing in Lake Pepin, in the presence of increasing densities of *Dreissena polymorpha*. This exotic invader was first found in Lake Pepin in 1990 and has since become widespread and dominant in the lower one-half to one-third of the lake (Hart, 1999; James *et al.*, 2000).

Densities of *Dreissena polymorpha* did decline at one of the mussel beds for unknown reasons. Possible causes for this decline may include a loss of a veliger source to repopulate the bed or changes in the chemical composition of the water above the bed (Mellina and Rasmussen, 1994). The first explanation seems most plausible, since densities of *D. polymorpha* were found to be lower in the upstream portion of the lake. Consequently, a large veliger source has yet to be located above this particular mussel bed (Hart and Davis, personal observation). As of 2000, *D. polymorpha* is found in excess of 20,000 individuals/m^2 in the lower one-third of the lake (Davis, personal observation). Densities of *D. polymorpha* at sampled mussel beds in this region of the lake are increasing rapidly, completely covering some portions of the lake bottom (Hart, 1999;

James *et al.*, 2000). Measurements of survival rates of native mussels in Lake Pepin indicate that, as in other parts of *D. polymorpha's* North American range (Haag *et al.*, 1993; Gillis and Mackie, 1994), *D. polymorpha* colonization is beginning to play a role in the decline of native mussel populations (Hart, 1999; Hart *et al.*, 2001a, 2001b).

Unfortunately, while declines in some population densities of unionid mussels, especially *Amblema plicata*, in Lake Pepin can be directly attributed to infestations of *Dreissena polymorpha* at this time (Hart, 1999), this mortality factor, unlike commercial harvest, cannot be controlled by natural resource managers. Furthermore, if the population declines that we measured were a direct result of *D. polymorpha*, we would have measured declines in all size classes of *Amblema plicata* as well as declines in population densities of non-harvested species. During this research this broad decline in mussel populations was not evident. Declines in the populations we studied were selective, i.e., most of the declines were attributed to loss of harvest-sized or near harvest-sized *A. plicata*, and not the other species in the community. Therefore, additional research is needed to determine the harvest impact upon *A. plicata* in the Upper Mississippi River, in particular Lake Pepin. This additional research should include a comprehensive population estimate of *A. plicata* in Lake Pepin that could be used in conjunction with recent estimates of *D. polymorpha* densities in Lake Pepin (James *et al.*, 2000). The findings of the present study, along with population estimates of *A. plicata* and *D. polymorpha*, should be incorporated into management objectives and harvest regulations formulated to ensure the continued survival of the unionid mussel communities residing in Lake Pepin.

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